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VOLUNTARY STRENGTH AND FATIGUE

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In voluntary efforts it is not known for certain whether the force that can be exerted is limited by the capacity of the nervous centres and conducting pathways to deliver motor impulses to the muscle fibres or by the intrinsic contractile properties of the fibres themselves; whether, in fact, a voluntary effort can be bettered by maximal tetanic stimulation of the muscle electrically, or not. Again in fatigue it is undecided whether tension falls because the degree of voluntary innervation drops or because the fibres are biochemically incapable of maintaining their contraction. The experiments described here attempt to settle these questions by comparing directly voluntary tension with that resulting from electrically excited motor volleys. To make a valid comparison in an intact human subject is difficult, but it will be argued that it can be achieved by using a particularly convenient muscle, the adductor of the thumb, and special apparatus.

The paper falls into three parts: the first shows that a maximal voluntary effort develops the same tension as a maximal tetanus artificially excited; in the second part the same equality is found to persist during fatigue, implying that in fatigue, too, the limitation of strength is peripheral; finally the effect of ischaemia is described. Preliminary accounts have already appeared (Merton & Pampiglione, 1950; Merton, 1950).

METHODS

The general arrangements for recording from the adductor pollicis are shown in Fig. 1. Maximal shocks were applied to the ulnar nerve at the wrist, the resulting action potentials led off by silver surface-electrodes and mechanical twitches recorded by a mechano-electric transducing valve (RCA 5734) and d.c. amplifier. Amplified action potentials and mechanical records were photographed on two cathode-ray tubes.

In experiments in which a very slow sweep was used, lasting several minutes, it was necessary to use a faint spot to avoid fogging. To obtain good photographic records of action potential height a diode valve was connected across the Y deflexion plates of the cathode-ray tube. Its effect is to rectify the negative phase of the action potential. This voltage remains on the amplifier output coupling condensers after the action potential and decays with a time constant of several seconds, determined by the condenser capacities and the resistances in the Y plate shift network. In this way the spot is made to move slowly enough to photograph, although the record then represents only the height of the first phase of the action potential. In these experiments time marking was done by a clock which connected a 12 V battery across the Y plates for a short time every 30 sec. This produced a dot below the action potential trace. When time marker and action potential coincided, the latter was lost, because of the low resistance of the battery.

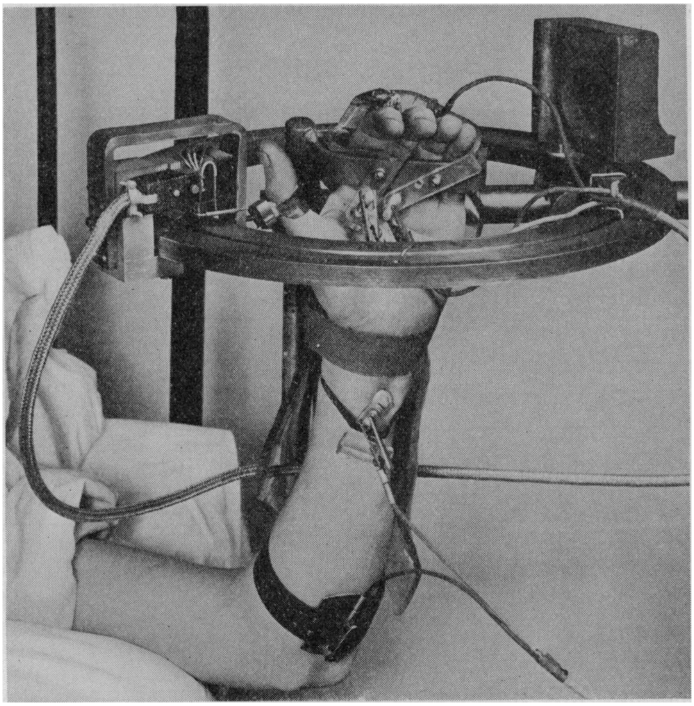

Fig. 1. Apparatus for recording simultaneous mechanical and electrical responses from the adductor pollicis. To the left, the mechano-electric transducer mounted on the outer track of a 12 in. ball-bearing. (Counterweight opposite takes up play in the race.) Silver lead-off electrodes on the palm and a wire running to an earthing pad behind the knuckles. Stimulating and indifferent electrodes on the forearm. The whole apparatus is mounted on a steel pillar (not shown) at a height suitable for use interchangeably on either a patient in bed (as shown) or a sitting subject. Two extra straps holding the arm to the splint removed for photography.

The great advantage of the adductor pollicis muscle is that under appropriate conditions it is the only ulnar-supplied muscle acting on the thumb and also the only muscle used in voluntary adduction. Thus voluntary force and the tension developed with electrical stimulation can be compared in reasonable certainty that the same muscle mass is producing both. The muscles that may interfere in the comparison by contributing to the voluntary tension are the median-supplied muscles of the thenar eminence (particularly the opponens pollicis), the flexor hallucis longus, and that part of the first dorsal interosseus muscle that arises from the first metacarpal. Steps were taken to minimize their actions as follows:

(1) The use of the muscles of opposition of the thumb was prevented by a device of which a photograph appears in Fig. 1. The splint which held the hand was attached to the inner track of

a 12 in. home-made ball-bearing. The outer track carried the tension recorder which could thus move freely around the hand. The axis of rotation was approximately coincident with the third metacarpal, the bone from which the adductor pollicis arises. When this muscle contracted there should, therefore, be little tendency for the race to turn. The opponens muscle, however, passes to the palmar side of the axis, and when it contracts the race should turn in the direction of thumb opposition. In practice, the line of the axis was so adjusted that when the ulnar nerve was tetanized alone the race took up a position with the thumb a little forward of the plane of the palm, but when the median nerve was simultaneously excited a large movement of opposition took place. With brief voluntary efforts it is found that the tension that can be exerted is not obviously increased by the use of the opponens if the race is free to turn. Presumably both muscles are then working at a lesser mechanical advantage. If the race is clamped, use of the opponens gives about a 30% increase in tension. When fatigue of the adductor has occurred the opponens can augment the tension even with the race free; for this reason the subject kept the thumb in the adductor position. Examination with a needle electrode confirmed that this procedure prevents significant use of median-supplied muscles, even when the adductor itself is grossly fatigued.

Owing to inertia the race cannot respond immediately to use of the opponens. Thus transient false increases of tension are still possible; for this reason brief peaks in a voluntary tension record are ignored.

(2) The action of flexor pollicis longus was rendered inappreciable firstly by encouraging the subject not to flex the phalanges of the thumb, and secondly by an automatic compensation in the tension recorder. The latter consists of an inverted steel U-member disposed so that the pull of the thumb diverges the limbs (Fig. 1), the transducer measuring this divergence. For a given force the largest reading is obtained when the direction of pull is not parallel to the line joining the ends of the limbs but makes an angle of about 30° above the horizontal, as seen in Fig. 1. When the proximal phalanx is flexed, however, the line of pull becomes more nearly horizontal so that the same tension produces a smaller deflexion on the record. The dimensions of the system are such that the maximum tension a subject can record is little affected by flexion of the phalanges, the increase due to use of the long flexor being offset by the less effective direction of pull. (If, however, the tension recorder is inverted so that the compensating action is reversed, the tension can be greatly augmented by flexing the thumb.)

(3) Any contribution from the first dorsal interosseus muscle was minimized by cutting away the splint so that there is nothing against which to brace the index finger, into which it is inserted. If, despite this precaution, a small component of tension from the interosseus still remains it is of little importance, for this muscle is also supplied by the ulnar nerve and therefore the comparison of voluntary and electrically excited contractions is not invalidated.

Observations on subjects making maximal efforts confirm the success of the apparatus in recording only the adductor pollicis. As he fatigues, a subject, in an attempt to restore the tension, may call into play forearm muscles, twist the hand about in the splint, flex fingers and thumb, etc. But so long as he pulls in the correct direction, as evidenced by the position of the ball race, these endeavours are strikingly ineffective at increasing the tension. This is true even when fatigue has reduced the tension of the adductor to a tenth or less of its full value. At such a time any contributions from extraneous muscles would have a relatively much greater effect.

In all the records illustrated here the subject was the author, but the principal results have also been demonstrated on other subjects.

RESULTS

As soon as the apparatus was put into use two facts were at once apparent; that there is a definite 'ceiling' to voluntary pull and that the sensation of effort and tension are completely unreliable. In a typical sequence the 'ceiling' tension is reached by what appears to be quite moderate exertion: the subject, unconvinced, then determines really to pull as hard as he can, the teeth clench and muscles all over the body are recruited in an intense effort, but in spite of strong subjective impressions to the contrary, the tension registered shows no increase; in fact after a few seconds it begins, with the onset of fatigue, to drop. Not, however, until it has fallen to a fraction of its initial value does the subject become aware that his strength is failing.

The tension 'ceiling' was very definite in Wilkie's (1950) experiments on the arm flexors. He noted that maximal movements could be repeated with great consistency over a period of months. He concluded on these and other grounds that in a maximal effort the degree of excitation of the muscles was constant. I have made similar observations on the adductor. Granted, then, that the maximal voluntary tension of a muscle has a definite and repeatable value, the next step is to compare it with electrical tetani. Wilkie could not do this but accepted the current view that the maximal tetanic tension would be larger. His paper, however, would actually gain in conclusiveness if it were shown to be the same.

Comparison of voluntary effort with tetanus

Records from a typical experiment are shown in Fig. 2, and the whole series is plotted in Fig. 3. First the subject makes a maximal effort lasting roughly a second ('Vol. 1'). After a minute's rest the response to a single maximal motor shock is taken (plotted as frequency 0 on Fig. 3). A minute later a tetanus at 10/sec is given, and after similar periods of rest, the other tetani at increasing frequency up to 50/sec. The 50/sec tetanus was then repeated with a 25 % larger shock to check that the stimulus was maximal for motor fibres. (Owing probably to polarization of the tissues the shocks must be more than double the voltage that is necessary for a single maximal response if they are to remain maximal throughout a tetanus at these rates. The considerable pain caused is minimized if the skin under the stimulating electrode is *not* broken.) Finally the voluntary effort is repeated to exclude the possibility of cumulative fatigue during the experiment ('Vol. 2').

The curve of tension against frequency of tetanus rises smoothly towards an asymptote along an S-shaped curve, in the way that Cooper & Eccles (1930) found in cat's muscles. The arrow on Fig. 3 is placed, as in their paper, at the frequency where the interval between shocks is equal to the contraction time of the muscle, i.e. the time from the beginning of the action potential to the peak of the twitch. This, as they found, is about half the frequency required to give a completely fused contraction. The tension attained with the faster rates of stimulation is closely the same as in the two voluntary efforts. There are good reasons for believing that the tetanic tension measured in this way is a true value, i.e. that stimulation was both sufficiently rapid and sufficiently strong to activate the contractile mechanism fully. (1) The tension was not increased by increasing the stimulating voltage; (2) the action potential size did not diminish during the tetanus. These two facts establish that the shock was

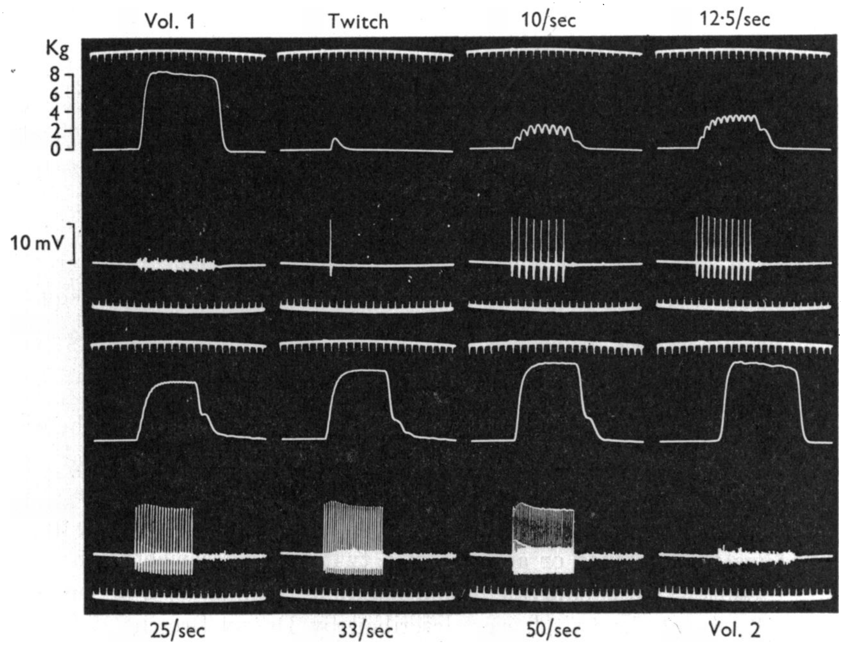

Fig. 2. Brief maximal voluntary efforts (Vol. 1 and Vol. 2) compared with a single maximal twitch and with tetani at the rates shown. Time markers, $\frac{1}{10}$ sec.

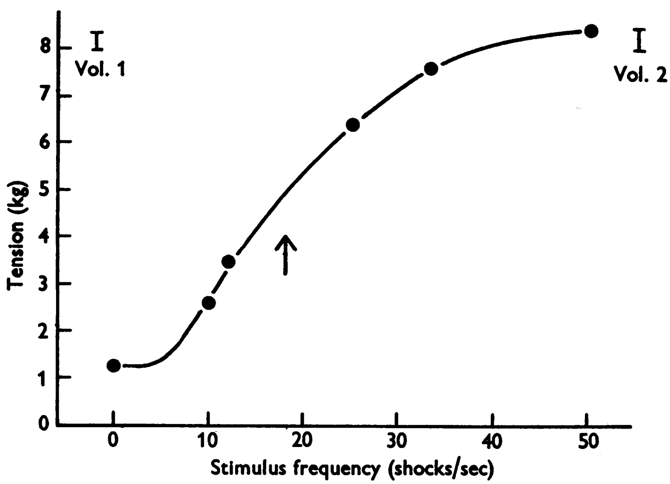

Fig. 3. The relation between tension and tetanus frequency and a comparison with two voluntary efforts (Vol. 1 and Vol. 2). A single twitch plotted as frequency 0. (Measurements of the records shown in Fig. 2.)

maximal. (3) At the highest frequencies the tension/rate curve in Fig. 3 has clearly flattened out. (4) At these frequencies the contraction is completely fused. (5) From Cooper's & Eccles's work it is known that nearly the full tension is developed in a tetanus with shock intervals equal to half the contraction time of the muscle. This rate was exceeded. For these last three reasons it is thought that the rate of stimulation was adequate to evoke a maximal contraction. As regards the voluntary contractions, the evidence that the tension recorded is produced only by the adductor has been given in the section on Methods. The conclusions from this experiment, then, are that the tetanic tension of the muscle has been correctly measured and is equal to its maximal voluntary tension.

The superimposed twitch

An independent check on this result can be obtained by studying the effect of an electric shock to the motor nerve interpolated during a voluntary contraction. The principle of the method is that if all the muscle fibres are fully activated an extra motor volley will not superimpose any twitch on the tension record. Thus the presence or absence of a twitch decides whether or not a voluntary contraction is equivalent to a maximal tetanus. This phenomenon of the occlusion of the twitch was described by Denny-Brown (1928). The experiment can with advantage be put on a quantitative basis, and Fig. 4 shows the effect of an interpolated maximal shock at a number of different levels of voluntary tension. At each tension five records are superimposed. Measurements of these records are plotted in Fig. 5. It is clear that the size of the superimposed twitch falls off linearly with increasing tension. The extrapolated value of the tension for zero twitch tension agrees with the maximal voluntary tension. (The value is some 10% lower than that obtained in Fig. 2 owing to slight fatigue, each record of Fig. 4 taking about 15 sec to make.) Even when there is only a very small twitch the motor volley still gives rise to an almost normal synchronized muscle action potential, so there is no doubt that the stimulus has excited effectively. The disappearance of the twitch at the greatest voluntary tension means, therefore, that the contractile substance is activated maximally.

The peculiar value of this experiment lies in its indifference to just those conditions which must be satisfied before the previous direct comparison experiment can have significance. It is not necessary that the shock should be maximal for motor fibres: were it submaximal all twitches would be smaller and perhaps more difficult to detect, but by their presence or absence voluntary efforts could still be tested, even if the test were less sensitive. Nor does it matter if other muscles are used to assist in the voluntary contraction; if there is no superimposed twitch that still means that the main muscle is contracting maximally, for what the experiment decides is whether those muscle fibres whose motor nerve fibres are excited by the shock are contracting maximally. The number of motor fibres stimulated may be only a fraction of the total

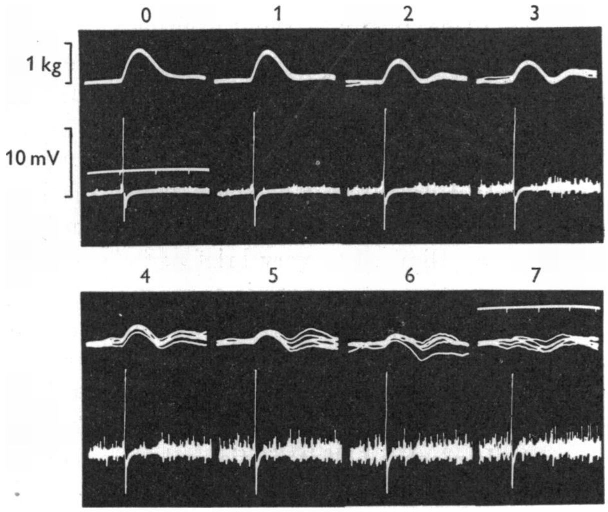

Fig. 4. Maximal twitches superimposed on steady voluntary efforts of the tensions shown (in kilograms) above each record. Lower traces show the corresponding action potentials. Camera shutter left open for five sweeps for each record. Time markers (on first action potential and last mechanical record), $\frac{1}{10}$ sec.

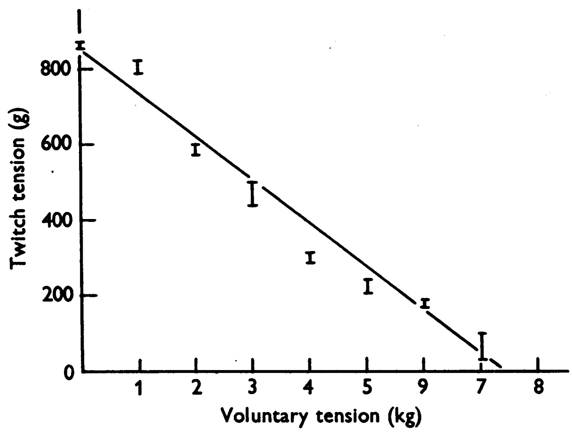

Fig. 5. The relationship between superimposed twitch tension and background tension (measurements of the records shown in Fig. 4). The vertical lines indicate approximately the total range of values of twitch height.

involved in the voluntary contraction, either because the shock is submaximal or because other muscles are being used which the stimulus cannot excite, but in the fraction caught by the shock those units which are not fully activated will give a twitch and those which are will not. This technique could, therefore, be applied in conditions like Wilkie's to test whether arm flexors were contracting maximally (Wilkie, 1950). It would be impossible to be certain of tetanizing all the flexors maximally (without exciting any extensors) in order to make the direct comparison, but a substantial fraction of the flexors could be stimulated by a single shock which is all that is needed for the present method.

Fatigue

In the experiments just described it has been shown that, contrary to the usual belief, a voluntary effort can realize the full tetanic tension of the muscle, but the observations were limited to very brief periods of contraction. It is a commonplace that our greatest strength is only available for a few seconds at a time before fatigue sets in, and this is readily confirmed with the present apparatus when an attempt is made to maintain contractions for longer. Indeed, if a maximal effort is recorded on a sweep sufficiently slow to see the whole course of fatigue the tension appears to drop linearly from the start (Fig. 6A, top trace). It reaches half its initial value in about a minute. The first question to be answered is whether the previous equality between voluntary and tetanic contraction persists or whether this falling-off represents a selective decrease of voluntary force with maintenance of the tetanus. If the equality still holds, then the site of fatigue must be peripheral to the point of tetanization of the nerve; otherwise it is central, wholly or partly. Experiment points definitely to a peripheral causation. At any point on the slope of decreasing tension an interpolated tetanus causes no return of tension. (The whole curve unfortunately cannot be obtained by tetanization because of excessive pain.) Similarly, single shocks superimpose no twitch. Thus, by the previous criteria, voluntary effort is continuing during fatigue to activate the muscle fully and the drop in tension must, therefore, be due to failure in some part of the peripheral apparatus.

If the subject begins at a smaller tension and holds it steadily as long as he can, at first interpolated shocks do cause twitches. As fatigue deepens the twitches get smaller and finally disappear. During this time the subject is making a progressively greater effort in order to maintain the tension. Finally, a maximal effort is needed and this corresponds to the time when the twitch disappears. Immediately afterwards the tension drops away along the usual fatigue slope.

Granted that the site of fatigue is peripheral, which part of the neuromuscular apparatus is affected? The only definite information offered here is from the muscle action potentials. During extreme fatigue they do not diminish in amplitude, so fatigue is not due to neuromuscular block. This is a point which has frequently been in dispute in animal experiments (e.g. Brown & Burns, 1949), but the answer here seems to be quite unequivocal. A complete experiment is illustrated in Fig. 6A. Maximal motor shocks to the ulnar nerve at the wrist are delivered at intervals of about 12 sec throughout.

Action potentials (of which, as already described, only the first phase is recorded) appear on the lower trace. At the start the tension record shows a number of maximal twitches. The subject then begins his voluntary effort, during which no superimposed twitches can be seen, but the corresponding action potentials are present, disturbed by voluntary potentials, but at approximately normal voltage. After the voluntary effort stops the first twitches are very small but they recover to normal in about a minute. Action potentials show no change during recovery but continue throughout at the initial

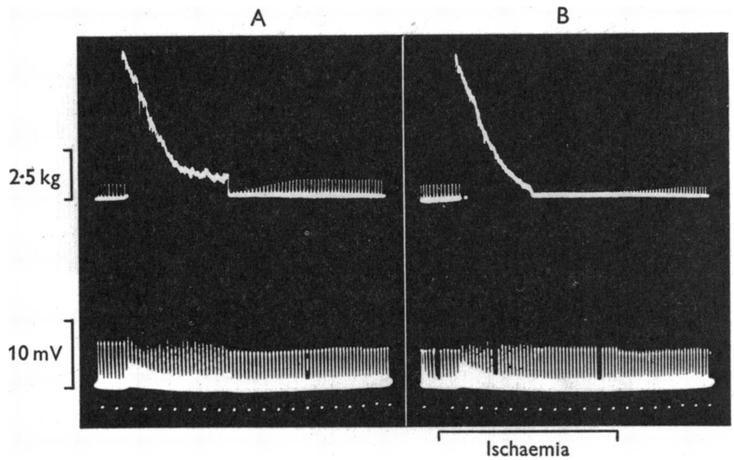

Fig. 6 A: a maximal voluntary effort persisted in until severely fatigued. A series of single twitches (evoked by nerve shocks) precede and follow. Lower trace, the corresponding action potentials, recorded as described under Methods. Time markers, ½ min. B: the same but with the circulation occluded for the period indicated by a line beneath the record.

amplitude. It appears therefore that a very large fall in the contractile power of the muscle during fatigue occurs without appreciable impairment of conduction from nerve to muscle. This conclusion is also implicit in the findings of Hoffmann (1919).

There exists the possibility that the action potentials recorded whose size does not diminish are not those of the muscle fibres that are suffering fatigue but perhaps come from a superficial piece of muscle which is little exerted: this seems unlikely because the adductor is the only ulnar supplied muscle near the electrodes and the preceding experiments claim to have shown that the whole of the adductor is involved in the contraction recorded. Nevertheless, the precaution was taken of recording from different parts of the adductor with a needle electrode: the results never differed from those already described.

A very similar picture is obtained if the muscle strength is judged by brief maximal voluntary efforts (Fig. 7A) or by brief tetani. After the fatiguing contraction, strength recovers rapidly, more rapidly in fact than the maximal twitch tension (cf. Fig. 6A). This difference in recovery rates of tetanus and twitch, representing a temporary change of the tetanus-twitch ratio, is of interest because it is the exact inverse of the well-known post-tetanic potentiation of the twitch that is seen after brief voluntary efforts or tetani.

Not only the twitch and the instantaneous strength recover rapidly but also the ability to make another prolonged effort. In Fig. 7A a second voluntary contraction is made 80 sec after the end of the first. The area under the tension curve is about 75% of the first. The full course of recovery has not yet been followed.

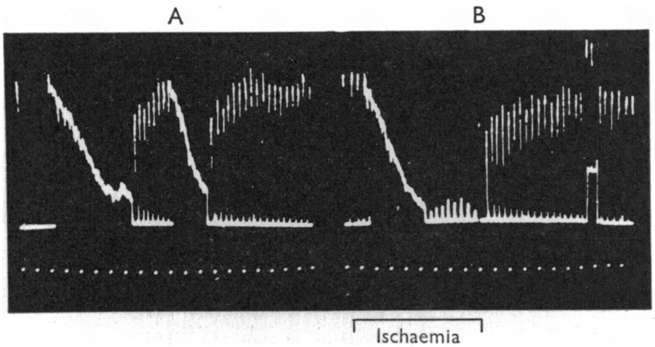

Fig. 7A: two prolonged maximal voluntary efforts, the second starting 80 sec after the end of the first. At other times strength tested intermittently by brief voluntary pulls. Time markers, ½ min. B: a single prolonged effort during circulatory arrest (indicated by the line below). Strength tested as in A. The pedestal towards the end of the record is an injected calibration signal equivalent to 2·5 kg.

Ischaemic fatigue

The simplest interpretation of the facts so far presented is that the biochemistry of the contractile process becomes defective during fatigue. Although normal action potentials pass over the fibres they cannot be made to contract. Recovery involves rest, and it will now be shown that it also requires a flow of blood, presumably to supply oxygen. In the ordinary fatigue experiment the tension falls linearly to about one-third of its initial value and then flattens out (Fig. 6A). The subject finds that he can keep up this low tension indefinitely, although with some little pain. If the circulation of the hand is cut off before the contraction begins by a blood pressure cuff inflated around the upper arm the initial part of the linear fall is the same, but it continues towards zero tension with little sign of flattening out (Fig. 6B). It is thought, therefore, that the flattening out takes place when the intramuscular pressure falls below systolic blood pressure, partial re-establishment of blood flow causing a slowing down of the fatigue process. When there is no circulation, fatigue can go on to extinction, but in practice severe pain makes the subject give up beforehand. If the circulation remains occluded, the muscle fails to recover until it is restored. This is shown when the muscle is tested by single shocks in Fig. 6B and tested for voluntary force in Fig. 7B. The same is true if tetani are used. These experiments show that recovery from this type of fatigue is essentially aerobic. As in aerobic records there is no diminution of the action potentials (Fig. 6B), so here again neuromuscular block does not occur.

This experiment is also important in giving an independent proof that fatigue is peripheral. If it were central, recovery should occur when effort ceases, for there is no interference with the circulation to central structures. But no strength returns until blood flow is restored to the hand and it must therefore be in the hand that fatigue has effect.

DISCUSSION

It is often held that in health the organs of the body such as the heart, liver, kidneys, skeletal muscles and perhaps even the cerebral cortex have at all times a large functional reserve. What the purpose is of a large functional reserve that can never be called upon is less considered. In the case of skeletal muscle this view is coupled with the belief that its potential strength is so great that if it were released tendons and bone would not be equal to the strain. It now appears that these fears and beliefs were unfounded. Maximal tetani do not tear the muscle from the bone but exert a force that can be matched by voluntary effort. It is true that maximal tetani are painful and feel to the subject to be much more powerful; in fact Hansen & Lindhard (1923) wrote: 'everyone who has experience of having his muscles stimulated by electrical stimuli knows that it is possible in this way to obtain contractions of a force which it is quite impossible to reproduce voluntarily'. Tension measurements do not confirm these subjective impressions, and it seems not unlikely that measurement would also upset the belief that lunatics, persons suffering from tetanus or convulsions or under hypnosis, and those drowning are exceptionally powerful. Cases where athletes and others snap their tendons or knee caps are probably to be explained by the forces, considerably in excess of the normal maximal tetanic tension, that muscles can be subjected to if they are stretched during a contraction. With fatigue there is an inconsistency in the current views, for whereas in running and other intense muscular efforts of the whole body it is accepted from the classical experiments of A. V. Hill and others that the supply of oxygen to the muscles is the factor limiting performance, in the case of small movements, such as the working of a finger ergograph, central fatigue or neuromuscular block are held responsible (Lovatt Evans, 1949; Bartley & Chute, 1947; Reid, 1928), although the evidence for these views has frequently been criticized (e.g. Lee, 1906). The present results seem to abolish the inconsistency by showing that blood supply is the significant factor even in contractions of a single small muscle. This conclusion may be artificial in a sense because the experiments lasted only a few minutes and the movement investigated involved little skill. Most small movements that are of practical interest as regards fatigue are skilful and repetitive for long periods, so that deterioration in performance may well be central in origin, but if the short-term strength of the muscles themselves is important, then the conclusions of this paper are relevant.

SUMMARY

1. In a muscle of the human hand voluntary strength is compared with maximal tetani, and the two are found to be equal.

2. During intense voluntary efforts electrical stimulation causes a normal action potential but no twitch. This is independent evidence that a voluntary contraction activates the contractile substance to the full.

3. Fatigue is peripheral, for when strength fails electrical stimulation of the motor nerve cannot restore it.

4. Neuromuscular block is not important in the fatigue of a volitional tetanus. Even in extreme fatigue action potentials evoked by nerve stimulation are not significantly diminished.

5. Recovery from fatigue does not take place if the circulation to the muscle is arrested. This again shows that the site of fatigue is peripheral.

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